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Critical trophic links in southern Chukchi Sea lagoons

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ABSTRACT

Arctic lagoons support a variety of fish, bird and marine mammal species, as well as subsistence fisheries that are critical to local food security along the Chukchi and Beaufort sea coasts. In summer 2015, diet samples from seven lagoon fishes were non-lethally collected in three lagoons along the Northwest Alaska coastline. Using these samples, we determined that the key prey species that supported these particular lagoon food webs were mysids, chironomids and Ninespine Stickleback. We identified the relative importance of freshwater/terrestrial and marine prey sources in lagoon fish diets and identified three key functional feeding groups of fishes: microbenthivore/zooplanktivores, macrobenthivore/piscivores, and piscivores. Several key predators were found in the microbenthivore/zooplanktivore group indicating a high degree of redundancy, which was lacking in the other functional feeding groups. This suggests that this group has the greatest resiliency, whereas other groups may be more vulnerable to changes in lagoon habitats. Functional groups with less redundancy, such as the upper trophic levels, may be good indicator species for identifying potential impacts to Arctic lagoons from climate change.

Coastal lagoons are dynamic transition zones between freshwater and marine ecosystems (Dürr et al., 2011), characterized by relatively shallow waters, high physicochemical variability (Barnes, 1980; Kjerfve, 1994), and connections to the marine environment that are either always, never, or periodically open (Kraus et al., 2008). The lagoon connectivity regimes dictate abiotic conditions and thus the species assemblages present (Kraus et al., 2002; Petry et al., 2016). During the ice-free season when lagoons are connected to the marine environment, they can become highly productive, well-mixed brackish water bodies (Dunton et al., 2012). The brackish lagoon waters allow epibenthic fauna, such as mysids and amphipods, to flourish (Craig et al., 1982; Griffiths and Dillinger, 1981). The high abundances of epibenthic crustaceans support Arctic fishes, migratory birds, and marine mammals (Dunton et al., 2012), several of which have key ecological and subsistence importance in the Arctic, including salmonids (both salmons and whitefishes), osmerids, and saffron cod, *Eleginus gracilis* (Logerwell et al., 2015).

In lagoons of the northeastern Chukchi and Beaufort seas, up to 90% of fish diets consist of mobile epibenthic crustacea, primarily mysids, with copepods, isopods and bivalves as the next most abundant prey items (Craig et al., 1982). For Arctic lagoon fishes, there is a high degree of omnivory, plasticity in feeding choices, and diet overlap among predator species (Craig et al., 1982; Harris et al., 2018). Classifying fishes into functional feeding groups enhances our knowledge of trophic dynamics by simplifying fish communities into guilds (Cummins, 1975), which group fishes together into groups that exploit common food sources (Fauth et al., 1996). From here, identifying the range and redundancy in functional feeding groups can provide a measure of resiliency of the ecosystem (Naeem, 1998; Walker, 1995), which is critically important to understand especially for Arctic ecosystems that are currently threatened by climate change and development.

Despite the importance of coastal Arctic lagoons throughout Alaska, food web structure and functional feeding groups have never been identified in these lagoons. In order to address this knowledge gap, our objectives here are to, 1) determine the diets of key lagoon fishes, 2) understand the importance of marine vs. freshwater/terrestrial prey sources for lagoon fishes, and 3) identify lagoon functional feeding groups and identify redundancy in the food web.

The Alaskan coastline of the southern Chukchi Sea is characterized by many periodically open lagoons, which frequently open in the spring and close during the summer and fall. We focused our studies on three lagoons, which span the range of conditions found across the coast. Aukulak, Krusenstern and Kotlik lagoons respectively have an area of 9 km^2, 60 km^2, 24 km^2 and had a mean salinity of 15.0 ppt (SD = 3.4), 1.8 ppt (SD = 0.6), and 14.7 ppt (SD = 4.9), in 2015. Previous studies have identified 7, 11, and 11 fish species in Aukulak, Krusenstern, and Kotlik lagoons respectively (Reynolds, 2012; Robards, 2014).

In summer 2015, we sampled fishes using experimental gill nets, fyke nets and beach seine sets. Gill nets were typically set and checked every hour, fyke nets every 3 h, and two beach seine sets were completed at each sample location. Diet samples were collected on an opportunistic basis from fishes caught during sampling. Fish selected for

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Table 1
Origins of prey items found in fish diets in the study lagoons.

Prey source	Prey item
Marine	Amphipoda, Bivalvia, Copepoda, Crangonidae, Euphausiacea, Isopoda, Mysida, Tubenose Poacher
Freshwater	Ninespine Stickleback, Pond Smelt
Terrestrial	Chironomidae, Diptera

Table 2
Definition of the functional feeding groups and species associated with each group in the study lagoons.

Functional feeding group	Definition	Species in group
Microbenthivore/zooplanktivores	Feed on benthic, epibenthic and hyperbenthic fauna, including invertebrates, as well as zooplankton, with prey sizes <1 cm	Humpback Whitefish, Least Cisco, Pacific Herring, Ninespine Stickleback
Macrobenthivore/piscivores	Feed on benthic, epibenthic, and hyperbenthic fauna, including invertebrates, as well as small fishes, with prey sizes >1 cm	Starry Flounder, Saffron Cod
Piscivores	Feed mainly on fishes	Inconnu

diet sampling were anesthetized using a solution of Aqui-S 20E (www.aqui-s.com) before nonlethal stomach-content samples were collected via gastric lavage. Stomach contents were flushed into a 250 μm sieve, transferred to a Whirl-Pack and preserved in a 95% ethanol solution. Stomach contents were sorted with a dissection microscope into the lowest practical taxonomic level possible, measured to the nearest mm, and enumerated.

Prey items were categorized by primary habitat groups based on the macrohabitats in which they are typically found, including terrestrial, freshwater and marine (Table 1). These denominations were determined by the predominant habitat of specific genera or species identified during diet sample analysis, using Mecklenburg et al. (2002) for fishes and Vassilenko and Petryashov (2009) for invertebrates. Freshwater and terrestrial sources were considered one category due to the paucity of prey items found in these groups. The relative importance of specific prey items in fish diets was determined by percent occurrence of each taxa. The proportion of marine contribution to fish diets was calculated as

$$\%m = \frac{prey_m}{prey_{total}}$$

where $prey_m$ is the number of marine prey items and $prey_{total}$ is the total number of prey items in the diet samples for each predator species. We defined functional feeding groups based on a modification of Franco et al. (2008), classifying fish species based on their feeding habits and prey types into three groups: microbenthivore/zooplanktivores, macrobenthivore/piscivores, and piscivores (Table 2).

During sampling, we captured a total of 14, 17, and 20 fish species in Aukulak, Krusenstern and Kotlik lagoons respectively, thus expanding the known list of species for these lagoons (Reynolds, 2012; Robards, 2014; Table 3). Freshwater, brackish/estuarine, and marine fish species (as defined using Mecklenburg et al. (2002)) were identified in all three lagoons, with brackish species being most common. Of the fishes sampled, several key lagoon fishes were identified and had the greatest number of diet samples collected across all three lagoons: Pacific Herring *Clupea pallasii*, Humpback Whitefish *Coregonus pidschian*, Least Cisco *Coregonus sardinella*, Ninespine Stickleback *Pungitius pungitius*, Saffron Cod *Eligenus gracilis*, Starry Flounder *Platichthys stellatus*, and Inconnu *Stenodus leucicthyes*. Diet samples for Humpback Whitefish, Saffron Cod and Pacific Herring were collected from all three lagoons

Table 3
Fish species found in Aukulak, Krusenstern and Kotlik lagoons, including data from Reynolds (2012), Robards (2014) and this 2015 effort. The tendency of each species has been described as marine (dark grey cells), freshwater (white cells) or brackish (light grey cells). Brackish indicates species that are found throughout the gradient of freshwater to marine, with brackish waters frequently playing an important role in their life histories.

Family	Latin name	Common name	Tendency	Aukulak	Krusenstern	Kotlik
Ammodytidae	*Ammodytes hexapterus*	Pacific sand lance	Marine			P*
Agonidae	*Pallasina barbata*	Tubenose poacher	Marine			P*
Clupeidae	*Clupea pallasii*	Pacific herring	Marine	P*	P	P
Umbridae	*Dallia pectoralis*	Alaska blackfish	Freshwater	P		
Osmerideae	*Mallotus villosus*	Capelin	Marine		P	P
	Osmerus mordax	Rainbow smelt	Brackish	P*	P	P*
	Hypomesus olidus	Pond smelt	Brackish		P*	
Salmonidae	*Coregonus laurettae*	Bering cisco	Brackish	P	P	P
	C. nasus	Broad whitefish	Brackish	P	P	
	C. pidschian	Humpback whitefish	Brackish	P	P	P
	C. sardinella	Least cisco	Brackish	P	P	P*
	Stenodus leucichthys	Inconnu	Brackish		P*	P*
	Thymallus arcticus	Arctic grayling	Freshwater		P	
	Oncorhynchus gorbuscha	Pink salmon	Brackish		P*	P*
	Salvelinus malma	Dolly Varden	Brackish		P*	P
Gadidae	*Eleginus gracilis*	Saffron cod	Brackish	P*	P*	P
Gasterosteidae	*Gasterosteus aculeatus*	Threespine stickleback	Brackish		P	P*
	Pungitius pungitius	Ninespine stickleback	Freshwater		P	P
Cottidae	*Megalocottus platycephalus*	Belligerent sculpin	Marine			P
	Myoxocephalus quadricornis	Fourhorn sculpin	Brackish	P	P*	P
Pleuronectidae	*Limanda proboscidea*	Long head dab	Marine	P*		
	Platichthys stellatus	Starry flounder	Brackish	P*	P	P
	Pleuronectes glacialis	Arctic flounder	Brackish	P*		P*
	Pleuronectes quadrituberculatus	Alaska plaice	Marine			P

P indicates species present in lagoons; * indicates new species identified in the lagoons during the 2015 sampling period.

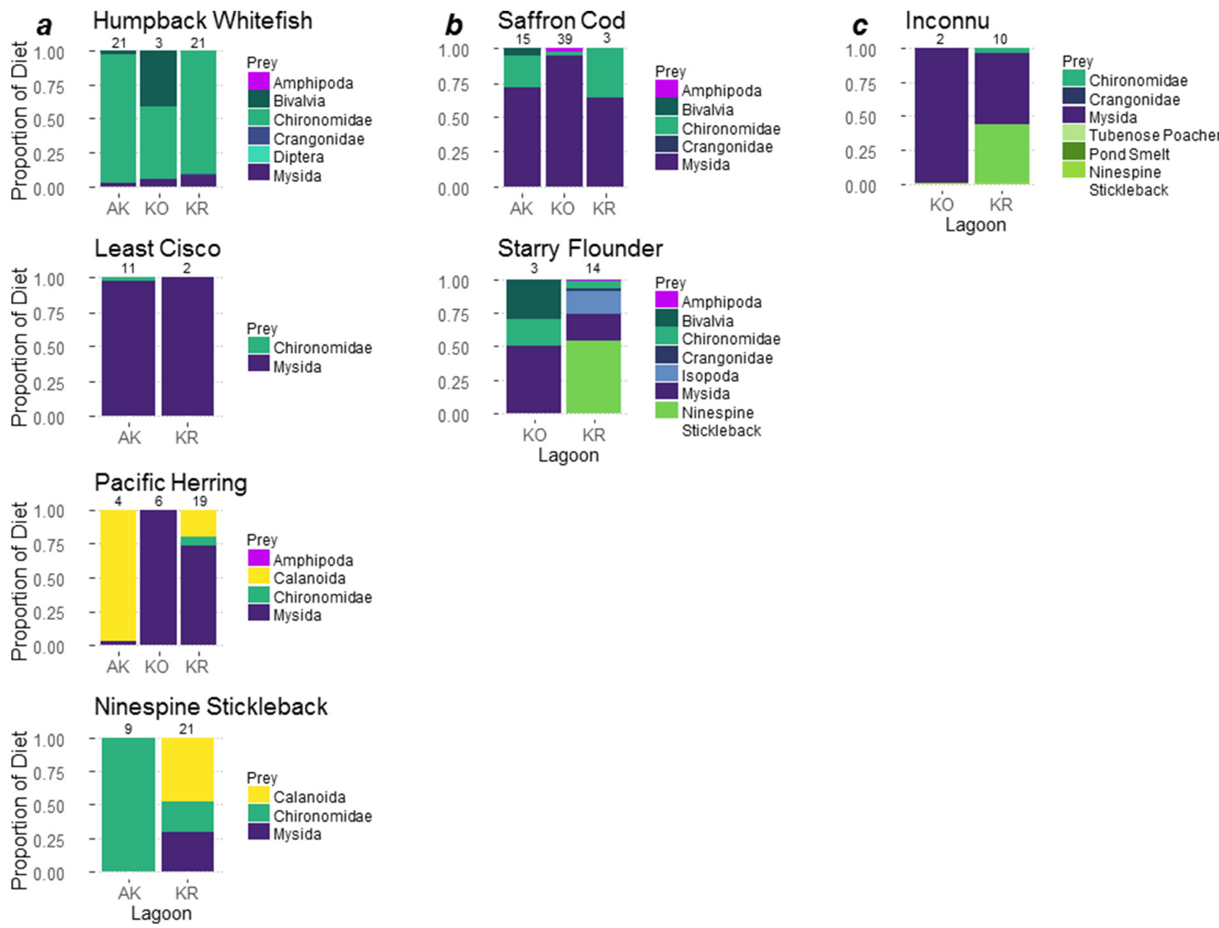

Fig. 1. Prey items consumed by the seven key lagoon fish predators, shown as the proportion of the total diet per species per lagoon for Aukulak (AK), Kotlik (KO), and Krusenstern (KR). The number of diet samples analyzed per lagoon is indicated above each bar. Each column of the figure indicates fishes in each functional feeding group: a, microbenthivore/zooplanktivores; b, macrobenthivore/piscivores; c, piscivores. Individual legends show the prey items that were consumed by each predator specifically.

and samples for Least Cisco, Ninespine Stickleback, Inconnu and Starry Flounder were collected from two lagoons. The disparity in diet samples collected across the three lagoons was due to not all species being abundant in all three lagoons.

Fishes consumed a wide variety of prey items, including crustaceans, invertebrates, and fishes (Fig. 1). Two main prey items dominated diets:

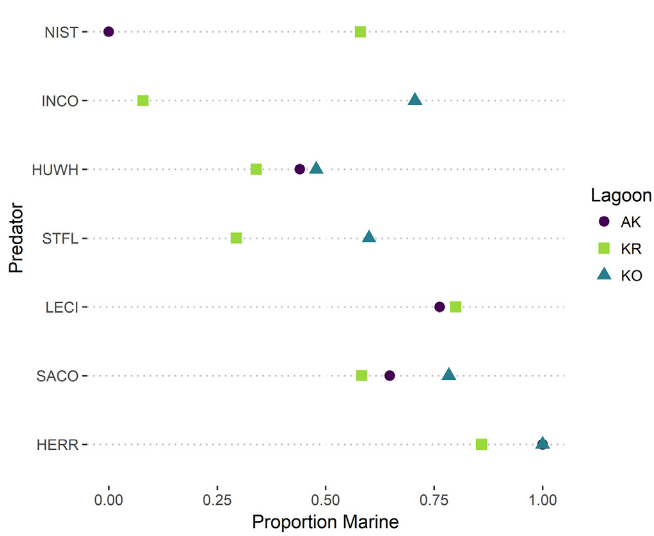

Fig. 2. Proportion of total diet comprised of items of marine origin for seven key predators for the lagoons in which diet samples were collected.

mysids and chironomids. These prey items were found in all species' diets and frequently made up over 90% of the diet contents. Amphipods were another important prey item, though less prevalent. Finally, Ninespine Stickleback were a commonly consumed prey item for piscivorous fishes, especially Inconnu. The majority of prey items were of marine origin, with few prey items having terrestrial or freshwater origins. The only freshwater/terrestrial invertebrate prey items were chironomids and dipterans. We found lower proportions of marine-derived food items in the freshwater species, Ninespine Stickleback (%m = 29%; Fig. 2), as compared to the brackish fishes (%m = 51%) and the marine fishes (%m = 81%).

We identified three main functional feeding groups in the lagoons: microbenthivore/zooplanktivore, macrobenthivore/piscivore, and piscivore (Fig. 1). Pacific Herring, Ninespine Stickleback, Humpback Whitefish and Least Cisco were microbenthivore/zooplanktivores; Saffron Cod and Starry Flounder were macrobenthivore/piscivores; and Inconnu were piscivores. The small forage fish species, such as Ninespine Stickleback and Pacific Herring, fed predominantly on zooplankton, though also fed on chironomids and mysids in lagoons where they were locally abundant. The whitefishes, Humpback Whitefish and Least Cisco, generally fed on microbenthic organisms, such as mysids, chironomids, small bivalves and amphipods and occasionally fed on zooplankton. Saffron Cod and Starry Flounder fed on the widest variety of prey items, including larger invertebrates and fishes. Finally, Inconnu were the only piscivorous fish identified during sampling, feeding predominantly on Ninespine Stickleback, though smaller size classes also consumed mysids (Fig. 3).

Overall, we found that a mix of freshwater, brackish and marine fish species inhabited the three study lagoons, although community

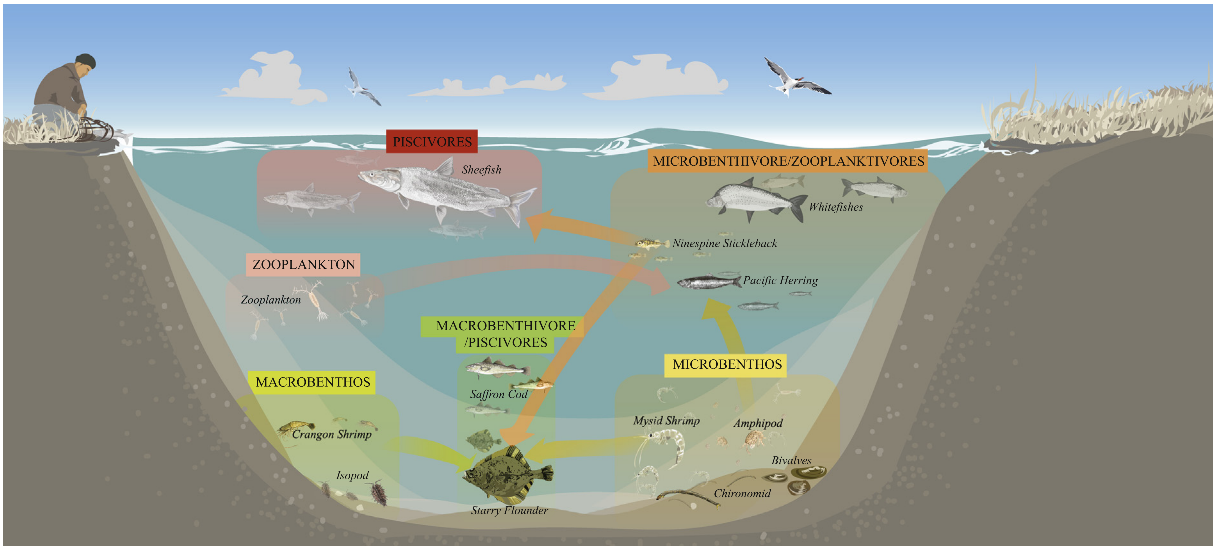

Fig. 3. A simplified graphical depiction of southern Chukchi Sea lagoon food webs, showing the key trophic relationships among the identified functional groups and prey groups.

composition was typically dominated by brackish water species. Most prey for these species were of marine origin with few terrestrial or freshwater contributors. The prevalence of marine origin prey suggests strong influences by adjacent marine communities rather than freshwater inputs to these generally brackish environments. The proportion of fish diets composed of marine prey items was generally high, though increased with the salinity tolerance of the fish species. This suggests that marine fish species target marine prey items to a greater degree than the brackish/freshwater fish species.

Of the three functional feeding groups, four of the seven predators were in the microbenthivore/zooplanktivore group, including two whitefish species analyzed, Humpback Whitefish and Least Cisco. The two predators in the macrobenthivore/piscivore functional feeding group, Saffron Cod and Starry Flounder, were opportunistic feeders, likely limited by gape width. These species fed on the widest variety of prey items, including larger epibenthic invertebrates, such as isopods and shrimps, and small fishes (Fig. 3). Ninespine Stickleback were an important prey for piscivorous fishes in the lagoons.

Within the functional feeding groups, a variety of prey items were targeted depending on species, particularly within the microbenthivore/zooplanktivores. There was more overlap between the two macrobenthivore/piscivore species. There was a high degree of redundancy within the microbenthivore/zooplanktivores, with four of seven predators analyzed located in this functional feeding group. A lesser degree of redundancy was found in the macrobenthivore/piscivores, and no redundancy was found in the piscivores. Because redundancy is a measure of resiliency to change (Walker, 1995), microbenthivore/zooplanktivores may have greater resilience to change compared to the other functional feeding groups.

The Arctic is experiencing the impacts of rapid climate change and increases in human development. The forecasted increase in sea level coupled with rises in storm action and coastal erosion may lead to increased lagoon barrier breaching changing the physical aspects of lagoon habitat (Haines and Thom, 2007; Jones et al., 2009). Increased accessibility of the Arctic may lead to new opportunities for development of resources and transportation corridors with potential oil spills, habitat modification, increased pollutant and contaminant loads and eutrophication (Arctic Council Protection of the Arctic Marine Environment Working Group, 2009). Changes to Arctic lagoon ecosystems that impact key trophic components, such as mysids and chironomids, will likely have cascading impacts on the food web and for subsistence. Functional groups with less redundancy would likely be most impacted, suggesting the upper trophic levels, such as Inconnu, may be good indicator species for change in Arctic lagoons. Long-term monitoring will be key to help identify opportunities to mitigate changes as they begin to occur in these critical ecosystems.

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